

Previously unnamed Australian *Drosera* and their published names.

The following list is compiled from Allen Lowrie's book, Vol. 2 and a formal description will be written by Dr. Neville Marchant at a future date. This list was sent in by Gordon Snelling.

- D. barbiger*a Planchon = syn *D. drummond*i
D. callistos = *D. sp.* 'The Lakes' (State Forest, Brookton Hwy.)
D. closterostigma = *D. sp.* 'Cataby'
D. coolamon = *D. sp.* 'Kalbarri'
D. echinoblasta = *D. sp.* 'camallo'
D. eneabba = *D. sp.* 'eneabba'
D. enodes = *D. sp.* 'Omissa-Marchant'
D. ericksonae = *D. sp.* 'Erickson's-omissa'
D. helodes = *D. sp.* 'bullsbrook'
D. hyperostigma = *D. sp.* 'platy-O'brien'
D. leioblasta = *D. sp.* 'Steve's-placea'
D. manniana = *D. sp.* 'Bannister'
D. nitidula ssp. *omissa* x *D. occidentalis* ssp. *occidentalis* = *D. sp.* 'Lake Badgerup'
D. occidentalis ssp. *australis* = *D. sp.* 'South coast'
D. omissa = *D. nitidula* ssp. *omissa*
D. oreopodion = *D. sp.* 'Armadale'
D. rechingeri = *D. sp.* 'Regan's Ford'
D. roseanal = *D. sp.* "Steve's-dichro"
D. spilos = *D. sp.* 'muchea'
D. walyunga = *D. sp.* 'Walyunga' (National Park)

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Evolutionary Patterns in *Drosera*

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Quite astonishingly, the *Drosera* of section *Thecalyx* still have the same primitive, strictly penanemere flower as *Aldrovanda*. There are two representatives: *D. sessilifolia* St. Hil. (South America) and *D. burmanni* Vahl (Australia, S.E. Asia, and India). The latter species has not clear-cut annual cycle and no specific mechanisms to survive droughts. When its substrate, usually well drained sand, shows the slightest signs of drying, the plant flowers. Then it just dies as soon as the seeds are ripe and only the latter survive the dry season (ASHLEY, 1975). This modulation of growth and flowering by droughts is typical of many tropical plants (RICHARDS, 1973, p. 66). Being a tropical plant, *D. burmanni* is not very likely to have reached Australia with the Antarctic migration. As a primitive species contrasting strongly with the sophisticated Australian sundews, it must have arrived quite recently (via Africa and Asia?). Its chromosome number ($2n = 20$) (VENKATASUBBAN, 1950) still is the same as in many South American species.

The second simplest flower structure has three (instead of five) unbranched styles. This we find in *D. meristocaulis* from Cerro de la Neblina in Venezuela, the only (surviving) member of its homonymous section. This is an odd-looking plant. Its ascending long oblanceolate leaves on a ramified stem and the axillary flowers remind one of *Drosopyllum* (MAGUIRE & WURDACK, 1957).

Another group with 3 simple styles is section *Psychophila*, with *D. uniflora* Willd. in the cold Southern parts of South America and, amazingly, two members in New Zealand: *D. stenopetala* Hook. and *D. arcturi* Hook. The latter is also found in the mountains of Tasmania and S.E. Australia. Depauperate forms of *D. stenopetala* resemble *D. uniflora* very much (DIELS, p. 65). These species must not have changed much since the Antarctic migration. The chromosome number of *D. arcturi* ($2n = 20$) links this section with South America (KONDO & WHITEHEAD, 1971).

The African equivalent of these species is *D. regia* Stephens, which was originally included in section *Psychophila*. A. A. OBERMEYER (1970) would rather place it in a section of its own. Yet the behavior of *D. regia* resembles that in section *Psychophila*. In *D. arcturi* a small area of the stem near the leaf bases swells up in Autumn, a possible equivalent of the *D. regia* rhizome. Smallish leaves are produced until the plant is covered with snow (MULLER, 1974; COTTER, 1986). *D. stenopetala* also forms small leaves in early Fall (BIRMINGHAM & COTTER, 1983). Significantly, so does *D. regia* (ZIEMER, 1980; SMYTHE, 1986). This species' biotope is cool and humid, one single mountain locality at an altitude of 1000 m. which is now the last refuge of this species since Africa drifted toward the equator.

These primitive remnants of the temperate climate *Drosera* announce changes in floral structure observed elsewhere. The styles are long and straight in *D. regia*, still undivided in *D. stenopetala*, but in some flowers of *D. arcturi* they show a tendency towards the basal bifurcation which is constant in *D. uniflora*.

The same 3 basally bifurcated styles (with two undivided branches each) are typical of the section *Drosera*. The branches tend toward a distal thickening and cleaving. Only in *D. natalensis* Diels does one find a new bifurcation about half way up the branches, a feature announcing things to come.

Most South American and African *Drosera* belong to this section. The leaf morphology often reminds one of the forms in the more primitive sections, i.e., spatulate-cuneate leaves with short, ill-defined petioles (*D. brevifolia* Pursh., *D. cavennensis* Sagot, *D. panamensis* Correa & Taylor, *D. chiapasensis* Matuda, *D. montana* St. Hil., *D. pusilla* Hbk.). An evolution towards narrow leaves is frequent (*D. arenicola* Steyermark, *D. chrysolepis* Taubert, *D. colombiana* Fernandez, *D. communis* St. Hil.). *D. cendeensis* Tamaya & Croizat looks like the North American *D. linearis* Goldie, and announces the theadlike leaf of *D. graminifolia* St. Hil. Rounder leaf blades also appear (*D. capillaris* Poir., *D. esmeraldae* Maguire & Wurdack, *D. felix* Steyermark & Smith, *D. kaieteurensis* Brummer-Dinger). The beautiful species *D. villosa* St. Hil. has the approximate shape of the well known *D. capensis* L., and the other African rosetted species resemble their South American relatives.

The many caulescent species are an important African innovation (the American *D. intermedia* Hayne is not very spectacular). There are short stems such as in *D. capensis* (broad leaf), *D. hilaris* Cham. & Schlecht., *D. bequaertii* Taton, *D. humbertii* Exell & Laundon, longer ones (to 25 cm) in *D. katangensis* Taton, *D. affinis* Welw., *D. glabripes* (Harv.) Stein, *D. madagascariensis* DC. The most spectacular species is *D. elongata* Exell & Laundon, which reaches a height of 60-90 cm, climbing on grasses and shrubs like its Australian counterparts of section *Ergaleium*. With its very small elliptic leaves this is a unique plant indeed.

Thanks to the persistence of primitive forces and to the large number of species available, the section *Drosera* offers good material for gaining some insight into the evolutionary mechanisms. The basic chromosome number is $2n = 20$, as in *D. brevifolia*, *D. capillaris*, *D. intermedia*, all the North American species (KONDO, 1970) and probably many more.

Of frequent occurrence in plants is so-called polyploidy, i.e., a multiplication of complete chromosome sets. The supplementary genes are then free to mutate into useless intermediary stages which in the course of time may acquire new and interesting properties (OHNO, 1980). *D. capensis* (BEHRE, 1929) and *D. madagascariensis* (KRESS, 1970) are tetraploids: $2n = 40$ chromosomes. The linear form of the leaves of *D. capensis* may be related to this, for a possible tetraploid form of *D. linearis* is said to resemble the Cape Sundew (SCHNELL & SIVERTSEN, 1974). *D. aliciae* Hamet is an octoploid (80 chromosomes) (KRESS, 1970).

An astonishing fact is that the more chromosomes a polyploid has, the smaller these are, and the less D.N.A. each edition of the genome contains: 25% of the original quantity in tetra- and octoploids, 50% in triploids (ROTHFELS & HEIMBURGER, 1968). The sequences lost are probably more or less useless repeats (46-95% of plant D.N.A.). The loss of these redundant genes does not seem to harm the plant (JONES, 1978). The same observed in *Drosophyllum*, with $2n = 12$ very large chromosomes (BEHRE, 1929). The amount of D.N.A. per nucleus is 16 times greater than in the diploid species of section *Drosera* (ROTHFELS & HEIMBURGER, 1968): this is much more than is needed to code for proteins! The many repeats may have a regulatory function, for as in polyploids the cells and nuclei here are much larger than in other *Droseraceae* (BEHRE, p. 298).

D. anglica Huds. has 40 chromosomes, but as seen the field, this may be a hybrid between *D. linearis* and *D. rotundifolia* L. (both $2n = 20$). The resulting cross ($2n = 20$) is sterile but becomes fertile if the chromosome number is doubled through an embryological accident: **amphiploidy** (WOOD, 1955). Other possible examples of such a process are *D. collinsiae* (= *D. burkeana* x *D. madagascariensis*?) and *D. dielsiana* (*D. burkeana* x *D. pilosa*?) (EXELL & LAUNDON, 1956). *D. natalensis* Deils may be a hybrid also: its chromosomes are described as having an irregular behavior during (meiotic) cell division (OBERMEYER, 1970 quoting A. KRESS).

Another modification of the karyotype is chromosome fusion forming pseudoisochromosomes. These may be transmitted during meiosis in tetraploids (JONES, pp. 148-149). Possible examples of this are *D. cuneifolia* L. with $2n = 32$ chromosomes (KONDO, 1976) and *D. regia* ($2n = 34$ chromosomes) (BEHRE, 1929).

The most advanced African *Drosera* are the species of section *Ptycnostigma*: *D. cistiflora* L., *D. alba* Phillips, and *D. pauciflora* Banks EX DC. Their 3 styles are bifurcated at their base as in the preceding section, but the branches are themselves ramified. The chromosome number of *D. cistiflora* is $2n = 60$ (BEHRE, 1929) and this plant may be a hexaploid with a basic number identical to that in section *Drosera*. Together with the similar flower structure, this probably shows section *Ptycnostigma* to be a specialized branch of the latter. This is also borne out by the co-occurrence of the naphtoquinones plumbagin and 7-methyljuglone in *D. cistiflora* and *D. capensis*. The other African *Drosera* tested only contain the second compound (ZENK et al., 1969). The most prominent characteristic of section *Ptycnostigma* is the yearly production of a fleshy root into which the plant retreats during the dry season (DIELS, p. 34; DEBBERT, 1987).

Such adaptations to an arid climate are even more sophisticated in Australia where many species have mutated beyond recognition. This holds for their vegetative parts but also for their flowers and karyotypes.

The clearest example of flower evolution is found in section *Lamprolepis* with the majority of pygmy *Drosera* *D. platystigma* Lehmann var. 'sewelliae' still exhibits 5 styles. In some species an inconstant reduction to 4 styles (*D. occidentalis* Morrison, *D. parvula* Planchon, *D. pulchella* Lehmann) or even 3 (*D. dichrosepala* Turcz.) is observed. *D. leucoblata* Benth. has 3 to 4, the other species 3 simple styles (*D. barbigerata* Planchon, *D. nitidula* Planchon, *D. omissa* Diels, *D. paleacea* DC, *D. platystigma* Lehmann, *D. pycnoblata* Diels, *D. scorpioides* Planch.). The strange *D. pygmaea* DC has a truly tetramere flower and is therefore considered the sole species of section *Rorella*. The chromosome numbers are not primitive at all: $2n = 10$ for *D. paleacea* (KONDO & LAVARACK, 1984), 18 for *D. pulchella* and 28 for *D. pygmaea* (KONDO et al., 1976). These must be examples of advanced chromosome fusion in polyploids.

The adaptations of these two sections to aridity are remarkable too. The dwarfed rosettes hug the ground, where the dessicating wind is slowed down by friction. The prominent stipules serve the same function. The 'gemmae' are an even more sophisticated mechanism to survive the dry season, based on the production of tough buds which eventually become detached and regenerate a new plant each.

In section *Arachnopus*, *D. schizandra* Diels has very broad leaves, distally bifurcated styles and weird stamens. In the taxonomically somewhat uncertain *D. indica* L. the opposite is observed: the leaves are very narrow, the styles branch basally and the stamens look more like their equivalents in section *Drosera* too. *D. adelae* F. Muell. is intermediate in all respects and may therefore be an amphiploid between the two. Its red-flowered form (STUDNICKA, 1988) may be the corresponding hybrid. The fourth species is *D. prolifera* C.T. White with its well known shape. The styles bifurcations here are somewhat more basal than in *D. schizandra*.

North Australia harbours a group related to section *Drosera*: section *Lasiocephala*. The species are: the polymorphous *D. petiolaris* R. BR., the recently described *D. dilatato-petiolaris*, *D. falconeri*, *D. lanata* (KONDO, 1984) and, astonishingly, *D. neocaledonica* Hamet. The latter must have reached New Caledonia during the Eocene or Miocene, when the Coral Sea was still rather narrow (TERMIER & TERMIER, p. 89). *D. falconeri* resembles *Dionaea* and is sometimes considered as a kind of 'missing link' (MAZRIMAS, 1987). This does not seem likely if the *Dionaea* trap evolved under water. The flower structure of these species resembles that in section *Drosera*: basally bifurcated styles (but the branches themselves are again divided).

Section *Lasiocephala*'s defence mechanisms against droughts need not be as sophisticated as in Southern plants: the dry season here is the winter! The plants are often hairy, which again is a way to slow down the dessicating air flow by increasing friction. During the summer *D. petiolaris* forms a compact resting bud (LAVARACK, 1977).

Leaving aside for the moment one or the other odd sections, we finally reach the most advanced *Drosera* in the world: the subgenus *Ergaleium*, which has had time to differentiate into three sections: *Ergaleium*, *Erythrorrhiza* and *Stolonifera*. The most astonishing mechanism to resist summer droughts has been developed here. Soon after the plants come out in Autumn, they produce an auxillary branch of the stem. This (often subterranean) branch grows downwards, then its apex turns upwards and starts accumulating water and food reserves. At the end of the rainy season all parts of the plant die with the exception of the swollen underground stem apex which is called a 'tuber'. The next year, the apical growth point of the tuber resumes its activity. It produces a new stem, which gives off a branch, and the process starts all over again. Some species rely on the production of more than one replacement tuber rather than on seeds for propagation (*D. zonaria* Planch., *D. whittakeri* Planch., *D. erythrorrhiza* Lindl. and to a certain extent *D. stricticaulis* (DIELS) O. H. SARGENT).

There is no need here to describe in detail the vegetative parts of all the species concerned. Section *Ergaleium* contains erect species, often climbers with wiry stems, or ramified ones. In section *Erythrorrhiza* all species have basal rosettes with unusually broad leaves. The fan-leaved sundews possess a basal rosette and stems with clasping leaves. The polymorphism of many of the species in all three sections is a sign that the evolution of these plants is still going on (DIELS, p. 45). As to the flowers, the styles here are often extremely ramified and bushy.

Few chromosome numbers have been determined: in section *Ergaleium* *D. auriculata* Backh. and *D. peltata* Smith have 32 (KRESS, 1970), *D. gigantea* Lindl. 28 (KONDO, 1976) and *D. menziesii* R. BR. 26 (KONDO, 1973). *D. whittakeri* Planch. from section *Erythrorrhiza* has $2n = 28$ chromosomes (KRESS, 1972). These all seem to be polyploids with subsequent chromosome fusion.

The odd species *D. hamiltonii* C. Andrews also has 28 chromosomes (KONDO, 1976) and is sometimes described as being close to section *Erythrorrhiza*, but without a tuber (CLEMESH, 1974; SLACK, 1979). This relation is not at all confirmed by the floral structure: this species has three rather unique fused styles similar to *Dionaea*'s and justifying its classification in a separate section *Stelogyne*. No modern Australian species possesses a flower structure which could have produced *D. hamiltonii*'s (DIELS, p. 48), except maybe the pygmies with 3 simple styles(?).

D. glanduligera Lehmann, the only member of section *Coelophylla*, has curious concave leaves which look like tiny scoops. This shape is very rare and reminds one of many *Drosera* of section *Ergaleium*.

There are other parallels with these. Certain species of section *Ergaleium* flower at the end of the season just before dormancy (ROSE, 1977). This may be a primitive trait already mentioned in tropical *Drosera*. *D. glanduligera* also flowers and dies when its surroundings become dry (CLEMESH, 1974), but if this does not happen, the plant is said to live through the summer, having then formed a very small, whitish tuber (NASH, 1973)! The flower has dichotomously ramified styles like many species in the subgenus *Ergaleium*. The seeds take up to two years to germinate as in the latter (NASH, 1973). This could be an adaptation to bushfires (LAMPARD, 1987). All in all this species may well be an example of what the ancestors of the tuberous sundews looked like.

Sources:

- ASHKEY, George (1975) *Drosera burmanni* in Queensland, Australia. CPN n°4:47-48.
BEHRE, Karl (1929) Physiologische und Zytologische Untersuchungen ueber *Drosera*. Planta (Berlin) 7:208-306.
BIRMINGHAM, Grant L. & COTTER, Phil C.P.'s of the Southern Alps of New Zealand. CPN 12 n°4:85-87.
CLEMESH, Stephan (1974) Notes on Australian *Droseras*. CPN 4 n°4:52-54.
COTTER, Phil (1986) *Drosera arcturi*. Bull. Assoc. DIONE (France) n°9:8-9.
DEBBERT, Paul (1987) *Drosera zeyheri*. Das Taublatt Vo. 8 n°2:9.
DIELS, L. (1906) *Droseraceae*. in: A. ENGLER (ed.) Das Pflanzenreich. Leipzig.
EXELL, A.W. & LAUNDON, J.R. (1956) New and noteworthy species of *Drosera* from Africa and Madagascar. Bol. Soc. Brot., ser. 2 n°30:213-219.
JONES, Keith (1978) Aspects of chromosome evolution in Higher Plants. in: Advances in botanical Research Vol. 6:120-198.
KONDO, Katsuhiko (1970) Chromosome numbers in *Drosera* and *Dionaea* in N. Carolina. J. Jap. Bot. Vol. 45 n°5:139-144. (through CPN 1 [1972] n°1:12). - - (1973) Chromosome numbers of some *Drosera* taxa. J. Jap. Bot. Vol. 48:193-198. (through

- CPN 6 n°1:19). - - (1984) Three new species of *Drosera* from Australia. Bol. Soc. Brot. 57 n°2:51-60.
- KONDO, K. & SEGAWA, M. & NEHIRA, K. (1976) A cytotaxonomical study in four species of *Drosera*. Mem. Fac. Integr. Arts & Sc., ser. IV Vol. 2:27-36.
- KONDO, K. & LAVARACK, P. S. (1984) A cytotaxonomical study of some Australian species of *Drosera*. Bot. J. Linn. Soc. 88 n°4:314-334.
- KONDO, K. & WHITEHEAD (1971) Chromosome number of *D. arcturi* HOOK. J. Jap. Bot. Vol. 46 n°11:344. (through CPN 1 [1972]:30).
- KRESS, Alfred (1970) Zytotaxonomische Untersuchungen an einigen Insektenfaengern. Ber. Dtsch. Bot. Ges. 83 n°2:55-62. - - (1972) News and Views. CPN 1 n°2:23.
- LAVARACK, Peter S. (1977) Notes on *Nepenthes mirabilis* and other carnivorous plants in Queensland. CPN 6 n°3:49-50.
- MAGUIRE & WURDACK (1957) The Botany of the Guyana Highland. Part II. *Droseraceae*. Mem. N.Y. Bot. Garden Vol. 9 n°3:331-336.
- MAZIRMAS, Joseph (1987) Comments after summary of JUNIPER, 1987. CPN 16 n°2:57.
- MULLER, Peter (1974) *Drosera arcturi*. CPN 3 n°1:12.
- NASH, Ray C. (1973) Tuberos sundews in South Australia. CPN 2 n°4:63-65.
- OBERMEYER, A. A. (1970) *Droseraceae*. in: Flora of South Africa 13:187-201.
- OHNO, Susumu (1980) L'évolution des gènes. La Recherche (Paris) n°107 (January 1980):4-14.
- ROSE, Steve (1977) Notes on tuberous *Drosera* of Western Australia. CPN 6 n°3:51-55.
- ROTHFELS, K. & HEIMBURGER, Margaret (1968) Chromosome size and D.N.A. values in Sundews (*Droseraceae*). Chromosome Vol. 25 n°1:96-103.
- SCHNELL, Donald E. & SIVERTSEN, R. (1974) A late summer C.P. foray into Michigan and Ontario. CPN 3 n°4:61-62.
- SLACK, Adrian (1979) Some favourite sundews. (British) C.P.S. Journal Vol. 3, Winter 1979:7-9.
- SMYTHE, Victor (1986) *Drosera regia*. (British) C.P.S. Journal 10 n°1:11.
- STUDNICKA, Miloslav (1988) A new *Drosera* from the section *Arachnopus*? CPN 17 n°1:12-14.
- VENKATASUBAN, K. R. (1950) in: Chromosome atals of flowering plants (C. D. DARLINGTON & A. P. WYLIE) 1955, George Allen & Unwin Ltd., London.
- WOOD, Carol (1955) Evidence for the hybrid origin of *Drosera anglica*. Rhodora 57:105-130. (through SCHNELL & SIVERTSEN, 1974).
- ZENK, M. H. & FUERBRINGER, M. & STEGLICH, W. (1969) Occurrence and distribution of 7-methyljuglone and plumbagin in the *Droseraceae*. Phytochemistry Vol. 8:2199-2200.
- ZIEMER, Bob (1980) *Drosera regia*. CPN n°1:15.

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